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Chapter 4

Cortico-spinal synchronization during motor learning

The brain controls nothing – it transmits.

Ross Ashby

Abstract

Motor performance is accompanied by neural activity in various cortical and sub-cortical areas. This intricate network has to be delicately orchestrated. We analyzed the role of β -synchronization in motor learning using magneto-encephalography combined with electromyography. Cortico-spinal synchronization in the β -band was found to be of particular importance in establishing bimanual movement patterns in the context of a 3:2 polyrhythmic (isometric) force production task. Its dynamics correlated highly with the learning of this complex bimanual motor skill. We submit that the cortical dynamics entrains the spinal motor system by which cortico-spinal β -synchrony serves higher-level motor control functions as primary means of information transfer along the neural axis.

Oscillatory neural activity can be found at different frequency bands in various cortical and sub-cortical areas. These neural oscillations have to be accurately tuned to achieve proper macroscopic performance. When assessed by encephalography, oscillatory activity generally gives rise to synchronization within a neural ensemble or between ensembles (Salenius and Hari, 2003). Importantly, neurons synchronize their firing patterns in accordance with different behavioral states. Changes in instantaneous amplitude or power therefore reflect changes in local synchronization, *e.g.*, within a cortical area. In contrast, changes in instantaneous relative phase or coherence reflect changes in more global, distributed synchronization, *e.g.*, between cortical areas or between cortex and neural ensembles in the spinal cord. In fact, synchronized activity across neural networks is believed to offer an effective mechanism for information transfer, especially when discriminating between frequency- and phase-locked activity (Alegre and Artieda, 2000; Salinas and Sejnowski, 2001).

In the context of motor control, it has been suggested that synchronization at different levels along the neural axis constitutes an important vehicle for motor timing (Baker et al., 1999; Farmer, 1998; Schoffelen et al., 2005). Cortical-cortical and cortico-spinal synchronization have been observed for both rhythmic (Boonstra et al., 2007) and non-rhythmic tasks (Kristeva et al., 2007; Salenius and Hari, 2003) and may occur in several frequency bands (Cheyne et al., 2008), each of which has been linked to a specific functional role. To paraphrase MacKay: "Oscillatory signals around 10, 20 and 40 Hz in the sensorimotor cortex have been associated with constant sustained muscle contractions. The dynamic phase at the onset of an intended movement is preceded by a marked drop in power, but not all frequencies are suppressed. Fast gamma (above 30 Hz) rhythms coincide with movement onset. Oscillatory signals even at low frequencies (between 4 and 12 Hz) may be linked to dynamic episodes of movement. These appear to exert preparatory functions. The neurogenic component of physiological tremor, an 8 Hz signal, is emerging as a factor in shaping the pulsatile dynamic micro-structure of movement, possibly in coordinating diverse actions." (MacKay, 2005). Cortico-spinal synchronization in the β -band is often associated with movement initiation and may also play an active role in postural stabilization (Androulidakis et al., 2007; Baker et al., 1999; Gilbertson et al., 2005; van Wijk

et al., 2009). Does this imply that β -activity is also relevant for motor learning?

To test for a significant role of β -synchrony in cortico-spinal systems in the context of motor learning, we studied synchronization while subjects learned a complex motor skill in which isometric forces had to be generated with the right and left index fingers at a fixed 3:2 polyrhythm. We previously investigated steady pre and post learning conditions (Houweling et al., 2008b), which revealed sustained changes in primary motor areas and in the cerebellum, even in control tasks that had not been learned. Synchronization patterns within and between oscillatory activities in these areas differentiated to distinct frequency bands. Here we report the dynamics of motor learning and delineate the characteristics of synchrony that co-vary with the observed changes in behavior, *i.e.*, with the achievement of proper motor timing. We expected cortico-spinal synchronization to increase with motor learning.

4.1 Materials and Methods

Experimental setup and design

Nine subjects (6 male, 3 female) exerted rhythmic isometric flexion forces with their left and right index fingers. Subjects gave their written informed consent prior to the experiment, which was conducted in full compliance with the guidelines of the Medical Ethical Committee of VU University Amsterdam. We recorded whole-head MEG (151-channel, CTF Systems Inc.) using 3rd-order synthetic gradiometers, EMG of the extensor digitorum communis and flexor digitorum superficialis, as well as the produced forces. All signals, including acoustic stimuli, were low-pass filtered at 400 Hz prior to digitization at a rate of 1250 Hz. All signals were mean-centered and high-frequency noise was eliminated using a 2nd-order bi-directional Butterworth low-pass filter at 400 Hz. In addition, EMG signals were high-pass filtered at 10 Hz and rectified using the Hilbert transform (Myers et al., 2003); see also below. To reduce computational costs, the signals were down-sampled to 250 Hz.

Subjects practiced a right:left = 3:2 polyrhythmic force-production task (40 trials of 45 s, each with 36 motor events of the left finger, total duration \approx 40 min). Frequencies for the right and left fingers were 1.2 Hz and 0.8 Hz, respectively. Pacing of the right hands frequency was provided at the right ear (EARTone 3A,

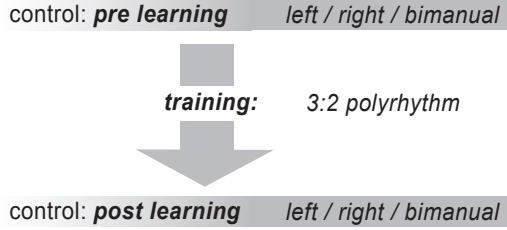


FIGURE 4.1: Experimental design: the training session consisted of 40 trials with 3:2 polyrhythmic force-production. Two sets of pre and post trials with ‘simple performances’ were conducted before and after learning: 2×8 unimanual and 1×8 isofrequency bimanual — see text for further details.

Cabot Safety Corporation, pitch 440 Hz, tone duration 50 ms). To facilitate learning we displayed two disks on a monitor that rotated at the movement frequency of the right index finger (right disk) and at $3/2$ of the frequency of the left index finger (left disk) this comparably simple visual target can be considered to simplify the complicated motor performance (Houweling et al., 2008b; Mechsner et al., 2001). That is, the two disks rotated at the same frequency when the proper rhythm was produced (see Fig. 2.1). In effect, we provided visual feedback by mapping all performances, including the 3:2 polyrhythm, to the simple 1:1 coordination.

As discussed in Houweling et al. (2008b) unimanual and bimanual isofrequency control conditions (8 trials of 25 s in each condition, see Fig. 4.1) served to detect pre/post learning differences in average power using a SAM beamformer approach (Veen et al., 1997; Vrba and Robinson, 2001). In brief, after filtering in the α (7–11 Hz), β (20–30 Hz) and γ (40–70 Hz) frequency bands, we identified the (sub-)cortical motor network by locating the sources showing the largest power changes (Cheyne et al., 2006; Houweling et al., 2008b). Next to increases in gamma power from pre to post learning in bilateral cerebellum (CB_{right} and CB_{left}), we found decreases in power in bilateral motor areas ($M1_{\text{left}}$ and $M1_{\text{right}}$), both in β - and γ -bands. Each beamformer yielded weight factors with which MEG signals were projected to sources as mere weighted mean. An in-depth analysis of activities pre and post learning, *i.e.*, during unimanual and isofrequency control conditions, has been conducted by Houweling et al. (2008b). Here, we extend this study and assessed activities at and interactions between these

sources during learning. For this purpose MEG signals from the 40 learning trials were projected onto the aforementioned sources (M1_{left/right} and CB_{right/left}) and further analyzed in relation to the continuous changes in performance.

Performance curve

In order to quantify the overall effect of motor learning we indexed performance by the strength of frequency locking between left and right fingers. In particular, we used the rectified EMGs and computed the normalized spectral overlap between their spectral densities at the 3:2 ratio. The normalized spectral overlap provides the similarity Ψ_x^y between two power spectra P_x and P_y after rescaling the frequency axis by a factor $\rho = p:q$

$$\Psi_x^y(\rho) = \frac{2 \int P_x(\omega) P_y(\rho\omega) d\omega}{\int P_x^2(\omega) + P_y^2(\rho\omega) d\omega}$$

see Daffertshofer et al. (2000a) for more details. $\Psi_{\text{EMG}_{\text{left}}}^{\text{EMG}_{\text{right}}}(3/2)$ was computed for every trial yielding 40 values per subject. To average performance over the group, principal components analysis was applied by using the co-variances between subjects prior to singular value decomposition. The primary principal mode served as performance curve (and the factor loadings represent the individual subjects contribution to the overall performance). Subsequently, several learning-related outcome measures were correlated with this performance curve.

Motor performance

For the individual motor behavior we considered the produced force (integrated over a trial) and the spectral power of the rectified EMG at the required movement frequency, which represents the efficiency of motor timing in every trial. We computed Pearsons correlation coefficients between the performance curve and the force and between performance curve and timing efficiency for every subject. These coefficients were subjected to a permutation test to assess significance across subjects.

Spectral power

In order to investigate whether the pre/post power changes were an effect of dynamic adjustments during learning, we analyzed power changes in α (9-12 Hz), β (18-30 Hz) and γ (42-72 Hz) frequency bands. Per frequency band and trial we determined the power in cortical and subcortical motor areas, as quantified by the mean of the event-related amplitude over the time interval considered (see below). For each subject, we tested for learning-related linear trends in power in these frequency bands via Kendalls rank correlation. The correlation with performance was again assessed in terms of Pearsons correlation coefficients between the performance curve and the power curves for every subject. Kendalls and Pearsons correlation coefficients were subjected to a permutation test to assess significance across subjects (see above).

Event-related amplitude and phase uniformity

Event-related fields were analyzed as a function of time and frequency after disentangling phase and amplitude changes by computing the instantaneous phase $\phi(t)$ and amplitude $A(t)$ of the analytic signal $a(t)$ computed via the Hilbert transform $x_H(t)$ by means of

$$A(t) = |a(t)| \quad \text{and} \quad \phi(t) = \arctan' \left(\frac{\Re a(t)}{\Im a(t)} \right) \quad \text{with} \quad a(t) = x(t) + \frac{i}{\pi} \left(x(t) * \frac{1}{t} \right)$$

here denotes the quadrant corrected inverse tangent and $*$ refers to a convolution. The four source-projected MEG signals ($M1_{\text{left/right}}$ and $CB_{\text{right/left}}$) were filtered in 3 Hz frequency bands over the range 0-72 Hz and split into epochs of 1250 ms (equivalent to 1/0.8 Hz) centered about the maximal increase in left and right forces.

Amplitude

Per frequency band and block of 5 or 40 trials we determined the event-related amplitude, normalized by the range over trials per subject resulting in a pseudo-Z statistic, as a measure of local synchrony. With the 5 trial blocks we addressed learning-related changes over time and with the 40 trial blocks we covered the complete learning session for comparison. The amplitude modulation in M1s was quantified as the difference of the amplitudes a_{ERS} and a_{ERD} , where ERS

and ERD corresponded to the maximum and minimum deviations from the mean amplitude in the β -band, respectively. Per subject, the significance of ERD and ERS was determined using a one-sided t -test over all motor events in each block.

Phase

Contralateral cortico-spinal synchrony was studied via the relative phase between EMG_{right} and $M1_{\text{left}}$, and between EMG_{left} and $M1_{\text{right}}$, whereas ipsilateral cortico-spinal synchrony was assessed by the relative phase between EMG_{right} and $M1_{\text{right}}$, and between EMG_{left} and $M1_{\text{left}}$. Per frequency band and block of 5 or 40 trials, we determined for all these relative phases of pair-wise combinations of motor areas and EMG¹ the circular variance cv and circular mean cm as a measure of cortico-spinal and cortical-cortical synchrony (Mardia and Jupp, 1972). In general, for a discrete set of phases $\{\phi_1, \phi_2, \dots, \phi_N\}$ the first order statistics are defined via the Cartesian coordinates of the phases:

$$cv = 1 - \sqrt{C^2 + S^2} \quad \text{and} \quad cm = \arctan' S/C \quad \text{with} \quad C = \sum_{k=1}^N \cos \phi_k, \quad S = \sum_{k=1}^N \sin \phi_k.$$

We note that phase uniformity², defined as $1/cv$, is biased by the number of phases N ; hence the uniformity values were transformed to the Rayleigh statistic $2 \cdot (1/cv) \cdot 2N$. High phase uniformity values indicate strong phase clustering, and persistent phase clustering (over a period of time) indicates phase locking.

Furthermore, the delays between contralateral M1 and EMG were investigated using the empirical distribution of the cortico-spinal uniformity as a function of the corresponding delays by binning uniformity values. That is, the circular means were multiplied by $2\pi/f$ for each frequency band f resulting in delays for each time/frequency instance. Uniformity values were divided in 200 bins ranging from the minimum to the maximum value. The means over the delays corresponding to the time/frequency instances within a bin were matched. The delays corresponding to strong phase locking can be regarded as the preferred

¹Since no significant cortico-spinal uniformity between M1s and extensor digitorum could be found (see below), $EMG_{\text{right/left}}$ always refers to the EMG recorded from the flexors.

²Uniformity agrees with more recently employed phase coherence $\frac{1}{N} |\sum_{k=1}^N e^{i\phi_k}| = \sqrt{C^2 + S^2}$; see Mormann et al. (2000).

delays.

To finally assess the correlation with performance, we performed regression analysis over all subjects and blocks with frequency locking at 3:2 as predictor and the maximal uniformity values or amplitude modulation as response. The regression was cross-validated by calculating the shrinkage factor S : each subject was consecutively removed from the sample and its response estimated by the regression equation. The shrinkage factor is the difference between the coefficients of determination of the original regression and the regression performed on the estimated responses with the observations (Osborne, 2000).

4.2 Results

Motor performance

One subject was not able to execute the unimanual control task, and one subject continued to perform very poorly as the mean of the 3:2 frequency locking values for this subject deviated more than two standard deviations from the overall mean. Both subjects were therefore discarded from source reconstruction and subsequent analyses. The overall change in performance for the remaining seven subjects is illustrated in Figure 4.2. Timing adjustments in the left finger were mainly responsible for improvement as the spectral power at the movement frequency of EMG_{left} correlated strongest with performance with a mean Pearson's correlation coefficient of 0.60 ($p < 0.001$) compared to 0.34 ($p < 0.001$) for EMG_{right} . Force did not show any significant correlation with learning: 0.13 ($p = 0.047$) for the left forces and 0.25 ($p = 0.08$) for the right forces.

Power changes

The SAM analysis of the control conditions identified systematic activity changes in various cortical and cerebellar motor areas (Houweling et al., 2008b). The largest, significant power decreases between pre and post unimanual conditions were found in the M1s opposite to the moving finger in all frequency bands. The largest, significant power increases were found in the cerebellar hemispheres. In agreement with these SAM results, we found that during learning, the mean event-related gamma amplitude, representing the average power during a movement cycle, decreased in the M1s (see Fig. 4.3A). In contrast, the event-related

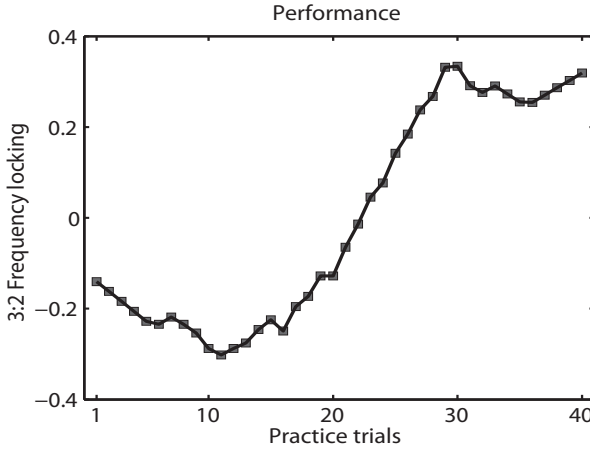


FIGURE 4.2: Frequency locking strength as a function of practice trials: principal component analysis (Marques de Sá, 2003) revealed the primary mode explaining 71% of the total variance; the eigenvector coefficients of the first mode were 0.67, 0.43, 0.11, 0.44, 0.38, -0.07 and -0.2 for subjects 1 to 7, respectively.

amplitude increased in the cerebellar hemispheres during learning. These power changes occurred primarily in the alpha band, but extended to the β - and γ -bands. The alpha power in cerebellar areas correlated weakly, but correlated significantly with performance, while β -power did not correlate with performance (see Fig. 4.3B). In CB_{right} , the gamma power correlated positively with performance as well. The power in both motor areas did not show any correlation with performance.

Amplitude modulation and uniformity

All subjects showed significant ($p < 0.01$) β -phase uniformity in the event-related patterns covering the complete session in the analysis (see Fig. 4.4C). Event-related β -amplitude modulation was also significant in all subjects (see Fig. 4.4A). Contralateral cortico-spinal phase synchrony was more pronounced for the left performances, as indicated by significant phase uniformity between $M1_{right}$ and EMG_{left} in the β -band (18-30Hz) and around the movement frequency, but not in the γ -band (40-70Hz). Significant ipsilateral cortico-spinal synchrony in the β -band was observed in two subjects, but no EMG-EMG uniformity was found.

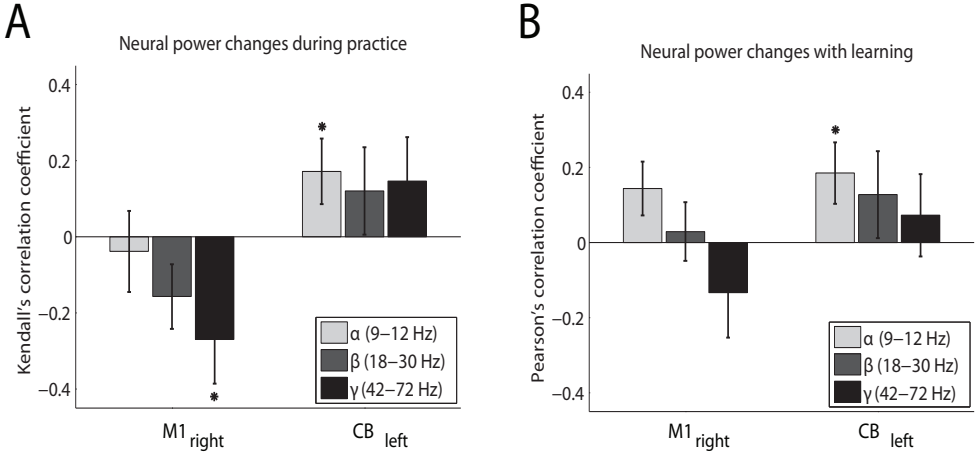


FIGURE 4.3: Power changes in M1_{right} and CB_{left}. Panel A: linear trends in power during learning in α -, β - and γ -frequency bands. The bars display the mean Kendall's correlation coefficients; the vertical line indicates its standard error (* corresponds to $p < 0.05$). Panel B: correlation between performance and power in α -, β - and γ -frequency bands. The bars display the mean Pearson's correlation coefficients; the vertical line indicates its standard error (* corresponds to $p < 0.05$).

In the EMG we observed an event-related modulation of β -amplitude in addition to the burst which accompanied the motor event. The modulation had distinct timing properties and closely matched the β -modulation pattern observed in M1 (Fig. 4.4B). Cortico-spinal phase uniformity correlated strongly with the modulation of the β -amplitude: periods of event-related synchronization in M1 coincided with the period of cortico-spinal synchronization, whereas during event-related desynchronization in M1 no significant cortico-spinal coupling was found (Fig. 4.4C). The localized distributions of uniformity values suggested a fixed, small delay between M1_{right} and EMG_{left} (Fig. 4.5A). Qualitatively the same results were found for EMG_{right} and M1_{left}, but in this case phase uniformity was in general weaker and less pronounced.

While the mean β -power decreased, the β -modulation $a_{ERS}-a_{ERD}$ in M1_{right} increased. That increase revealed a positive correlation, $\tau = 0.25$ ($p = 0.07$, $S = 16\%$) of M1_{right} amplitude modulation at the slow movement tempo with learning. The upper panels in Figure 4.5B illustrate this for Subject 4. The fig-

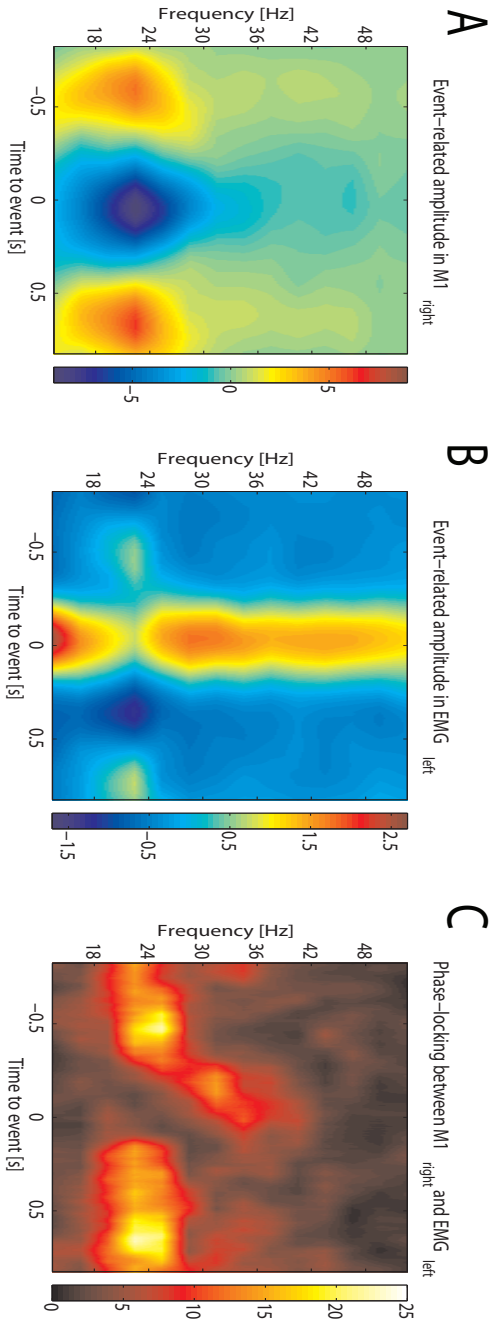


FIGURE 4.4: Panel A: event-related amplitude (pseudo- Z) of $M1_{right}$ in the time-frequency plane, averaged over subjects and events. Panel B: event-related changes in EMG amplitude (pseudo- Z): next to burst around the motor event, clear deviations from mean amplitude in the β -frequency band were observed (example: EMG_{left} in subject 4). In general, a deviation from the β -amplitude in the EMG is difficult to detect since the burst preceding the motor event has a much higher amplitude and spread across frequencies. Panel C: Rayleigh statistics of the relative phase between EMG_{left} and $M1_{right}$ in the time-frequency plane averaged over subjects indicating short phase locked episodes.

ure also shows the uniformity of the relative phase between $M1_{\text{right}}$ and EMG_{left} . The maximum of these uniformity values correlated positively with motor performance, $\tau = 0.50$ ($p < 0.001$, $S = 21\%$); see Figure 4.5C. For the uniformity between the phases of $M1_{\text{left}}$ and EMG_{right} , we found also a positive, but weaker, correlation with performance, $\tau = 0.39$ ($p < 0.001$, $S = 15\%$). The amplitude modulation $a_{\text{ERS}}-a_{\text{ERD}}$ at the fast frequency of β -oscillations in $M1_{\text{left}}$ also correlated positively but not significantly with performance, $\tau = 0.18$ ($p = 0.19$, $S = 13\%$). The α -modulation in CB_{right} showed a positive correlation with performance, $\tau = 0.3$ ($p = 0.03$, $S = 9\%$). This effect was absent in CB_{left} .

The cortical-cortical uniformity between M1s also showed event-related patterns; however, these patterns seemed to be subject-specific both in frequency and time, as well as degree of uniformity. High, significant uniformity values were consistently found around 10 Hz, 25-30 Hz and 45 Hz. These patterns revealed movement-related changes as they modulated with the movement frequency, but did not correlate with performance. However, the maximal uniformity values in the gamma band correlated negatively with motor performance, both for phases aligned to the right motor event, $\tau = -0.52$ ($p < 0.001$, $S = 20\%$), and to the left motor event, $\tau = -0.48$ ($p < 0.001$, $S = 20\%$).

4.3 Discussion

We studied neural synchronization in the α -, β - and γ -bands in establishing bi-manual movement patterns in the context of a 3:2 polyrhythmic (isometric) force production task. Cortico-spinal synchronization in the β -band was found to correlate highly with the learning of this complex motor skill. Our results support the pivotal role of properly timed and synchronized neuronal activity for motor control. We found intermittent phase locking episodes between β -oscillations in contralateral M1s and the corresponding EMG. Cortico-spinal phase locking occurred at small, distinct individual delays. The strength of the locking, quantified by phase uniformity, correlated with amplitude modulation and increased with improved performance so that accurately timed β -activity appears very important for achieving proper performance.

We extended our previous study (Houweling et al., 2008b) on dynamic after-effects following learning of the 3:2 polyrhythmic force-production task. The ob-

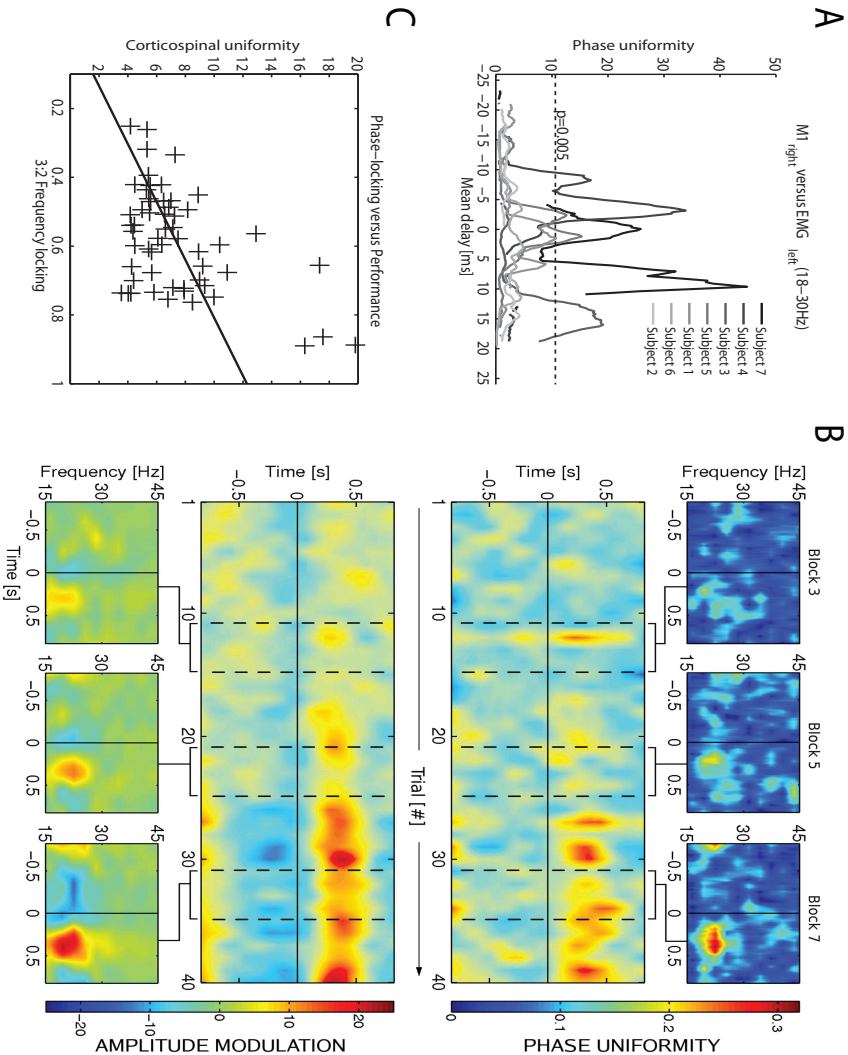


FIGURE 4.5: Panel A: distribution of transformed phase uniformity (Rayleigh statistic) as a function of the delay, *i.e.*, the corresponding circular mean transformed to the time domain. Each curve represents a single subject, showing the individually preferred mean phases. **Panel B:** learning-related changes in amplitude modulation (lower half) and cortico-spinal uniformity (upper half) in Subject 4. The three top and bottom panels show time/frequency patterns of blocks 3, 5 and 7, while the two middle panels zoom in on the β -band (18-30 Hz). **Panel C:** correlation between cortico-spinal phase uniformity in the β -band and learning, *i.e.*, the strength of 3:2 frequency locking (all subjects). To achieve reliable (*i.e.*, significant) estimates of the phases, we subdivided the 40 learning trials into 8 blocks of 5 trials (5 trials \approx 180 events).

served power decrease in M1s was probably an effect of practice, as we did not find any correlation with motor performance. The alpha power increased and alpha modulations in cerebellar sources correlated weakly with performance suggesting that the timing function of the cerebellum was involved in improving performance. The decreases in cortico-cortical synchrony in the gamma band were possibly related to attention, as we suggested in our previous study where these changes were found to be long-lasting and reported as an 'after-effect'. However, since this synchronization seemed to occur with zero phase delay, we have to be cautious in drawing this conclusion. Moreover, the decreases in gamma amplitude in both M1s suggest that the decrease in interhemispheric uniformity may be related to these power decreases.

In our previous study we also reported increases in phase uniformity between M1s at the movement frequency between isofrequency bimanual control conditions pre and post learning. As the event-related uniformity only measures 1:1 phase synchrony, and therefore appeared inappropriate to assess phase locking at the movement frequencies in M1s during polyrhythmic performance, we focused on frequency locking at 3:2 in the M1s (Houweling et al., 2008a). Even though we did not find an increase in 3:2 locking between M1s, the stronger increase of timing efficiency in the EMG_{left} (with respect to the EMG_{right}) was reflected in the power at the slow movement frequency in M1_{right}. Moreover, neural correlates of motor performance were found in the uniformity of the relative phases between M1s and between M1 and contralateral muscle groups. β -Phase locking between M1_{right} and EMG_{left} correlated stronger with performance than β -phase locking between M1_{left} and EMG_{right}. The asymmetry in adaptation is thus reflected in an asymmetry in the correlation of cortico-spinal synchrony and M1 oscillatory activities with performance.

The present results suggest that accurate timing of β -band activity is essential in motor control. The clear correlation between cortico-spinal phase locking and the amplitude modulation in contralateral M1 and its deceptive preference for distinct, brief delays suggest that phase synchronization may serve to encode and transfer information along the neural axis (Tass, 1999). Interestingly, the EMG revealed an event-related modulation of β -amplitude superimposed on the event-related EMG burst (Fig. 4.4B), implying a (nearly) zero-lag phase synchrony, that is, in-phase locking. In particular after learning, *i.e.*, during accurate

performance, synchrony-based motor control appeared brief and discrete despite the continuous, ongoing motor output. Whether this means that also rhythmic movements have a discrete neural foundation remains difficult to answer (Huys et al., 2008; Schaal et al., 2004). Here it appears relevant that fixed neural populations adjust their capacity to construct short epochs of synchronization leading to brief, and hence expedient, motor commands and accurate motor timing (Davidson et al., 2007).

We are inclined to argue that motor control is described best by mechanisms that are capable of responding instantaneously to changes in timing and feedback. Motor learning is facilitated by diligent adaptive control. Fast oscillators are capable of exchanging information at the time scale needed for motor control. If tightly phase locked, these oscillators can stabilize (bimanual) coordination (Daffertshofer et al., 2005). Put differently, during periods of strong synchrony the phase locking between (sub)systems increases and this mutual intermittent coupling generally supports the necessary information exchange. In the current experiment we found that the periods of strong coupling between muscle and motor cortex became more focused (both in time and frequency) when performance improved, which is consistent with this hypothesis. Thus, in view of its co-variation with both M1 (β -) amplitude and EMG (β -) amplitude, we conclude that phase locking reflects a neural control process by which M1 imposes its dynamics on the muscle.